has distinct spicules. The latter three species range in size from 1.5–4 cm; have one stone canal; one or two Polian vesicles; and are gray or brown in color (Table 1).

ACKNOWLEDGMENTS

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A NEW SPECIES OF SEA OTTER FROM THE LATE PLEISTOCENE OF NORTHWESTERN CALIFORNIA

FRANK H. KILMER[1]

ABSTRACT: A new species of sea otter is described from a Late Pleistocene marine deposit, Humboldt County, California. The species is closely related to the living sea otter, Enhydra lutris, but differs significantly in possessing larger P_3, P_4, M_1, and presumably M_2, shorter ascending ramus with respect to total length of mandible, and a more simply formed angle. Proportions of the mandible suggest that the skull of the new species may have been slightly longer and lower than that of E. lutris. No special affinities with particular living populations of E. lutris are recognized.

The prior fossil records of sea otter in the northeastern Pacific has, with but one exception, included only postcranial elements and all fossil discoveries have occurred in two widely separated areas, Oregon and southern California. The Oregon record consists only of a right femur of Pleistocene age from the Elk River Formation (Leffler, 1964). The southern California records (Mitchell, 1966) include a lower, deciduous tooth of Early Pleistocene age from the Timm's Point Silt, a right humerus of Late Pleistocene age from

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the Palos Verdes Sand, and various limbs and vertebral elements from Late Pleistocene deposits of Santa Rosa Island. Leffler referred the Oregon femur to *Enhydra* sp. while Mitchell concluded that all the southern California specimens probably were referable to *Enhydra lutris* (Linnaeus).

In May 1967, a well preserved mandible of a fossil sea otter, lacking only a few teeth, was recovered from a Late Pleistocene marine deposit, located on the Humboldt County coast, north-western California. The mandible is evidently the first known of a fossil sea otter from the north-eastern Pacific and it provides the first major indication of the cranial morphology of fossil sea otters. The Humboldt County mandible is interpreted to be that of a new species of sea otter referable to the genus *Enhydra*.

The left and right rami of the mandible were discovered at the same locality by different persons at different times. The close morphologic agreement of the two rami and near perfect fit of the symphysis make it virtually certain that they are from the same individual.

GENUS *ENHYDRA* FLEMING, 1822

Enhydra macrodonta, new species

Figures 1 and 2

Holotype: California State University, Humboldt, Department of Geology and Earth Science, specimen No. 745-1, a mandible lacking left P_2, M_1, and M_2; right incisors and M_2. The medial projection of both condyles has been broken off.

Type locality: California State University, Humboldt, Department of Geology and Earth Science, locality No. 745. A moderately steep, north-facing, excavated slope located approximately 11 miles north of Arcata, Humboldt County, California, at the junction of U. S. 101 and Crannell Road. The exposure consists of three, nearly flat-lying, sedimentary units including (from bottom to top): 1) a basal 12 feet of gray, medium-grained, pebbly, fossiliferous, semi-consolidated sand; 2) 50 feet of gray, clayey, fine-grained, fossiliferous sand; and 3) 70 feet of light-brown, medium-grained, semi-consolidated, pebbly sand.

The rami were found, as float, lying on the exposed surface of the gray clayey sand unit. The left ramus was found in a narrow gulley at the foot of the excavated slope about 230 feet east of the centerline of Little River Road (the frontage road for U. S. 101). The right ramus was found directly upslope from the left ramus a distance of approximately 25 feet. The gray, clayey sand matrix adhering to both rami is identical with the lithology of the gray clayey sand unit and it is virtually certain that the two were eroded from this stratigraphic unit.
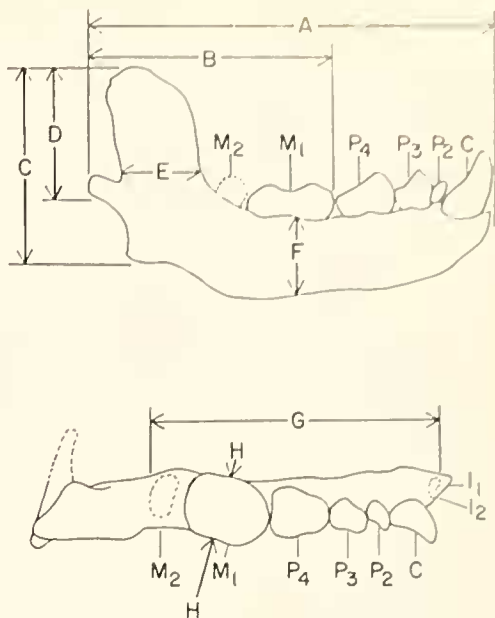

Figure 1.   Key to mandibular measurements utilized in this study and presented in Table 1. Dimensions A, B, and D are measured from the posterior margin of the condylar process along the axis of the ascending ramus. All measurements are in millimeters.

Formation: The otter-bearing unit has not been formally described or named and it can be definitely traced only about ¾ mile south of the Crannell Road locality. Its relationship with the well known Cenozoic sedimentary sequence (Ogle, 1953) exposed in the Eel River Valley 40 miles to the south is not known. However, reconnaissance mapping and indirect paleontologic evidence suggest that the otter-bearing unit may be older than the Hookton Formation (Late Pleistocene) and either younger or partially equivalent to the Carlotta Formation (Plio–Pleistocene); these formations are in depositional contact with each other in the Eel River Valley sequence.

Age: Late Pleistocene (see discussion below).

Diagnosis: Relative to *Enhydra lutris,* the only other species included in the genus: horizontal rami thick, occlusal outline of P_3, P_4, and M_1 approximately ⅓ larger and plump; M_2 presumably slightly larger based on slightly greater length and width of the alveoli; and ascending ramus short with respect to length of the mandible; angle sharply rounded, right-angled, with ascending and horizontal margins narrow and rounded.

Description and comparison: The close correspondence between the fossil mandible and those of the compared specimens of *Enhydra lutris* (Table 1) with respect to size, shape, and dental morphology indicates that *E. macrodonta* is closely related to *E. lutris* and is certainly assignable to

TABLE 1. Selected mandibular measurements of *Enhydra macrodonta*, new species and *E. lutris*. Key to measurements A–H is given in Figure 1. All measurements are in millimeters.

Spec. No.	Loc.	Species	Growth stage	Sex	A	B	C	D	E	F	G	H	$M_{\underline{2}}$ (alveolus) L	W	M_1 L	W	P_4 L	W	P_3 L	W
(a) 745-1	Calif.	*E. macrodonta*	Yng. adult	?	83.9	50.2	41.9	28.0	19.6	18.3	61.4	15.2	6.8	8.7	18.5	15.8	13.4	11.9	8.3	8.9
(b) M71-080	"	*E. lutris*	Adult	?	90.8	54.8	47.2	33.8	22.6	17.7	60.4	11.2	5.0	7.1	15.5	12.8	11.1	9.2	6.7	6.8
(c) 6902	Alaska	"	Adult	M	90.9	56.3	47.5	37.4	24.0	19.1	56.5	10.7	4.8	5.9	17.7	13.9	12.2	10.5	6.5	7.0
(c) 6801	Calif.	"	Adult	M	81.6	53.4	51.5	38.0	23.7	17.9	54.1	10.6	5.3	8.2	15.6	12.0	10.5	8.9	7.0	4.9
(b) M71-081	"	"	Yng. adult	?	86.1	54.3	45.5	34.2	23.9	18.7	54.1	10.9	4.8	6.8	15.4	13.7	10.7	9.6	6.1	6.9
(b) M71-082	Alaska	"	Adult	F	83.9	50.8	42.2	32.1	21.5	15.7	53.8	10.0	5.3	5.9	15.3	13.9	9.8	9.4	6.4	6.5
(b) M71-083	"	"	Adult	?	83.7	55.1	43.6	32.7	22.8	15.9	53.9	9.5	4.9	5.3	15.2	11.5	10.7	9.0	6.9	5.0
(b) M71-084	"	"	Adult	?	86.4	51.1	43.8	33.1	22.6	16.9	54.8	6.1	5.6	5.6	15.4	12.4	11.6	9.3	Badly worn	Badly worn
(d) 135831	Calif.	"	Adult	M	79.7	35.7	46.2	29.3	19.7	17.8	52.5	11.2	5.3	7.4	15.3	12.7	9.7	8.9	5.7	5.7
(b) M71-085	Alaska	"	Adult	F	86.4	50.4	44.5	33.8	22.6	17.2	54.3	10.6	5.3	6.7	14.4	12.8	10.8	9.4	6.4	5.3
(b) M71-086	"	"	Yng. adult	?	80.1	47.4	39.6	29.7	21.0	15.7	55.1	11.4	5.9	7.3	16.2	12.8	10.8	9.1	7.4	5.4
(b) M71-087	"	"	Adult	?	80.2	48.0	40.6	29.1	21.2	17.4	53.8	12.8	5.3	7.9	16.0	12.9	11.6	9.3	7.1	5.1
(d) 137003	"	"	Juv.	M	77.3	30.6	35.7	22.6	19.4	16.0	53.9	12.6	4.7	7.3	14.9	13.4	10.9	9.5	6.4	6.3
(b) M71-088	"	"	Juv.	?	75.8	45.7	39.5	29.5	18.4	16.9	52.6	12.4	5.3	7.3	17.1	13.4	*11.6	*9.4	7.4	5.9
(b) M71-089	"	"	Juv.	M	79.0	43.6	38.4	28.1	18.6	15.3	54.0	12.3	4.6	8.2	15.4	12.6	*10.8	*9.4	7.4	4.9
(b) M71-090	"	"	Yng. adult	?	75.4	43.4	38.4	28.5	18.3	16.0	53.6	12.7	5.5	7.9	16.7	13.1	11.4	9.6	7.6	5.5
(b) M71-091	"	"	Juv.	F	74.5	41.8	34.4	24.3	18.1	14.0	52.5	13.9	4.3	6.3	15.9	12.4	**	**	7.2	5.5

L. Length.
W. Width.
* Milk dentition.
** Unerupted milk dentition.

(a) Calif. State Univ., Humboldt, Dept. of Geology and Earth Science.
(b) Calif. State Univ., Humboldt, Dept. of Zoology.
(c) U. S. Geological Survey, Pacific Coast Center, Menlo Park, Calif.
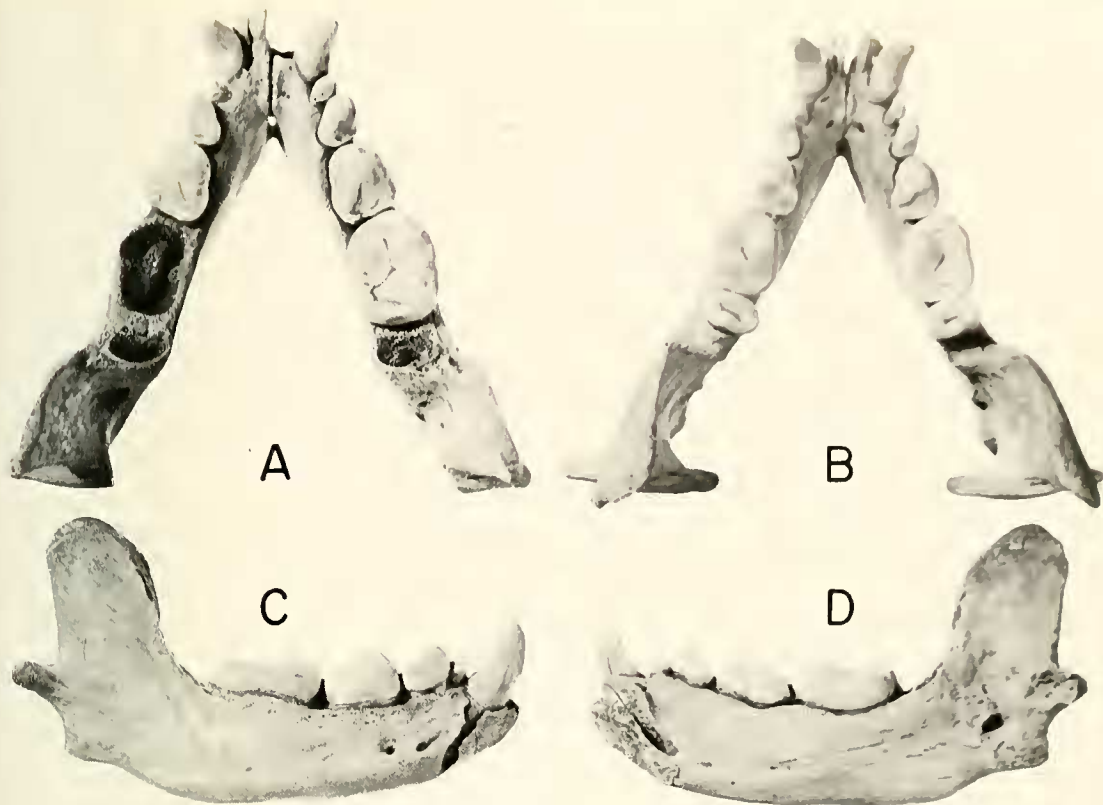(d) Univ. of Calif. Museum Vert. Zool., Berkeley, Calif.

Figure 2. A, *Enhydra macrodonta*, new species; joined left and right mandibular rami, occlusal view (CSUH, Dept. of Geology and Earth Science, No. 745-1). B, *Enhydra lutris* (Linnaeus); mandible, occlusal view (U.S. Geological Survey, No. 6801, adult male, Asilomar State Beach, Monterey Co., California, captured 14 April 1966). C, *Enhydra macrodonta*, new species; right mandibular ramus, lateral view (CSUH, Dept. of Geology and Earth Science, No. 745-1). D, right mandibular ramus, medial view (CSUH, Dept. of Geology and Earth Science, No. 745-1). Scale 1×.

the genus *Enhydra*. The presence of permanent dentition coupled with the lack of extensive wear suggests death at an early adult stage of life.

Although the gross morphology of the *E. macrodonta* closely resembles that of *E. lutris* it differs significantly from specimens of comparable or even greater jaw length in that the horizontal ramus is more robust and strongly built, to accommodate the larger teeth, and the toothrow is proportionately longer. The medial surface of the jaws tends to be rather flat and featureless as in *E. lutris* but the lateral surface differs in being less concave below P_3–P_4 and substantially more convex below M_1 and M_2. There are two large, oval-shaped mental foramina on each ramus below P_3 and P_4 on the lateral surface. These foramina are larger than the mental foramina seen in *E. lutris* but their location is essentially the same.

The ascending ramus is more lightly built, more slender, and shorter than those of *E. lutris* of comparable jaw length. The lateral and medial surfaces of the ascending ramus are essentially parallel and without the surficial irregularities typical of *E. lutris*. The anterodorsal margin of the coronoid crest is narrow and slightly curled medially whereas, in *E. lutris* the margin is more strongly curled and thicker. When the toothrow is placed in a horizontal position, the anterior edge of the ascending ramus rises at a steep angle and the posterior margin is nearly vertical. In this position the coronoid crest does not project posterior to the condylar process although it overhangs it slightly.

The masseteric fossa is a deeply excavated depression which shallows anteriorly, diminishing to an arrowhead-shaped point. The point is directed anteriorly, not downward as is common in *E. lutris* and terminates just below the posterior

half of M_1. In *E. lutris* the anterior extremity of the masseteric fossa almost invariably lies below M_2 and occasionally lies below the posterior margin of M_1. The condyles are about the same size and diameter as the largest specimens of *E. lutris* examined and they are connected to the posterior margin of the ascending ramus by strongly built gussets of bone. The angle consists of a narrow, sharply rounded corner, the posterior and ventral sides of which form an angle of about 90°. The backward-pointing, plate-like structure, which commonly forms the base of the angle in *E. lutris*, is absent in the Humboldt form.

The horizontal angle formed by the medial surfaces of the mandible, when the jaws are placed in the position of "best fit" at the symphysis, measures approximately 63°. Although the magnitude of this angle must be considered only an estimate, since the jaws were not found articulated, it is close to a number of adult specimens of *E. lutris* in which the same angle ranged from 56° to 60° (Fig. 2A, B).

Although the toothrow in *E. macrodonta* is significantly longer than in those specimens of *E. lutris* having comparable jaw length (Table 1), the teeth in the fossil are spaced and individually oriented in the jaws almost identically to those of the living species. The line of teeth form a fairly well-pronounced arc which bows outward in occlusal view. Whether this curvature is a reflection of growth stage or is a constant character is not certain; in adult *E. lutris* curvature of the toothrow also occurs but it seems to be much less pronounced (Fig. 2A, B).

The M_2 is lost in both left and right jaws of *E. macrodonta* but the alveoli are well-preserved and their size (Table 1) suggests that M_2 was slightly larger than that found in *E. lutris*. The alveolus of M_2 lies in a large, rounded bulge which swells medially from the base of the anterior edge of the ascending ramus. The alveolus is positioned considerably higher than that for the M_1. Its shape and orientation suggest that it was occupied by a single-rooted, ovate tooth, whose long axis was oriented transversely to the jaw and whose occlusal surface tilted forward at a moderate angle. The general orientation and position of the alveolus in *E. macrodonta* closely resembles that found in specimens of *E. lutris* in which the growth stage is considered to be late juvenile/early adult.

The M_1 is a bunodont tooth with the cusps arranged in a pattern almost identical to that of *E. lutris*. The tooth width and the distance between the protoconid and metaconid are, however, proportionately greater, and the occlusal area is

about ⅓ larger. The alveolus for M_1 in the left jaw is figure-eight shaped in occlusal outline. Near its center there are distinct inward projections of bone, one of which connects to a centrally located transverse ridge. This suggests that the alveolus was divided into anterior and posterior sockets as is standard in *E. lutris*.

The P_4 of *E. macrodonta* is approximately ⅓ larger in occlusal area than that of *E. lutris*. The constriction of the root, evident below the enamel base and above the alveolar margin, suggests that the tooth possesses two roots as in *E. lutris*. The occlusal morphology of the P_4 closely resembles that of *E. lutris* except that in *E. lutris* the ridge radiating posteriorly along the lateral side of the tooth is larger and developed into a more distinct cusp-like structure.

The P_3 in *E. macrodonta* has nearly twice the occlusal area of that in *E. lutris*. It is about ⅓ the size of P_4 but is similar in occlusal outline, the major exception being a more sharply rounded anterior corner. The low ridge on the medial side of the tooth is proportionately larger in *E. lutris* and it tends to be more inflated and cusp-like. The tooth is oriented as in *E. lutris* but does not appear to lean outward and overhang the jaw as is frequently the case in *E. lutris*.

The P_2 is about ⅙ the size of P_3 and is only slightly larger than P_2 in *E. lutris*. The long axis of the tooth crosses the jaw axis at an angle somewhat greater than in P_3. The tooth does not appear to be directed laterally nor to overhang the jaw to the degree as in *E. lutris*. A single, nearly round alveolus in the left jaw indicates that the tooth possessed one root, as in *E. lutris*.

The canine is almost identical in size and form to the canine in *E. lutris*. The first lower incisor of *E. macrodonta* is a long, slender tooth of which nearly half is exposed root. The cutting edge of the enameled surface is bluntly wedge-shaped, with the long axis oriented transverse to the jaw axis. The second lower incisor tightly fills a narrow space between I_1 and the canine. The wedge-shaped crown is about twice the length as that of I_1. Taken as a group, the close alignment of the canines and incisors suggest that the bite of the animal was effective across the entire anterior margin of the mandible. The incisors show very close correspondence in size to those in *E. lutris*.

DISCUSSION AND CONCLUSIONS

Taxonomic assignment: Enhydra macrodonta is assigned to the genus *Enhydra* because of its close

resemblance to *E. lutris* in both mandibular and dental morphology. It consistently and significantly differs from known or examined mandibles of *E. lutris* in the following features: 1) greater size of P_3, P_4, M_1, and possibly M_2; 2) longer toothrow; 3) a sharply-rounded angle formed of ascending and ventral margins which are narrow and rounded; and 4) shorter ascending ramus with respect to total length of mandible. These differences are interpreted as justifying the assignment of this fossil mandible to a new species.

Other morphologic characters which are, to some extent, duplicated in specimens of *E. lutris* include: 1) the masseteric fossa extends anteriorly to a point beneath the posterior half of M_1, and is anteriorly directed; 2) M_2 occupies a large, medially directed swelling, partially hidden from lateral view by the ascending ramus; 3) the medial and lateral surfaces of the ascending ramus are essentially smooth and without bulges or depressions; and 4) the margin of the coronoid crest is narrow and curled only slightly medially. These four characters may represent a transitional stage in growth or perhaps relate to sex and are, therefore, considered to be of questionable diagnostic value at this time.

Morphologically *E. macrodonta* is sufficiently close to *E. lutris* to indicate that the two species are closely related. However, the larger teeth and thicker jaw of *E. macrodonta* seem to suggest that *E. lutris* was, perhaps, not derived directly from *E. macrodonta*, but rather that the two species represent separate lineages which presumably had a common origin prior to the Late Pleistocene. One cannot rule out the possibility, however, that selection toward a "small-toothed" *E. lutris* might have occurred from a "large-toothed" *E. macrodonta*. If this selection did occur then the general tendencies during the evolution of *E. macrodonta* to *E. lutris* would have included: 1) reduction in size of P_3, P_4, M_1, and possibly M_2, with proportionately greater reduction in tooth width; 2) reduction in the thickness of the jaw below P_3, P_4, and M_1; 3) reduction in the length of the toothrow; 4) increase in the overall size and complexity of the ascending ramus; 5) increase in height of the ascending ramus with respect to total mandibular length; 6) development of stronger muscle attachments at the angle and ventral margin of the ramus; 7) maintenance of the same general size of incisors, canines, and P_2; and 8) maintenance of about the same orientation of the long axes of premolars and molars in occlusal view.

The suggestion by Fisher (1941), that the mandible in *E. lutris* might reflect an evolutionary process tending to progressively shorten the mandible, is generally supported by the present study. If, as Fisher suggested, the teeth have been progressively crowded together during the evolution of sea otters, so that their long axes now assume variable angles as they do in *E. macrodonta*, then that process probably began before the Late Pleistocene.

Enhydra macrodonta does not appear to retain characters which might provide clues into the pre-Pleistocene evolution of sea otters, nor does it seem to offer a test of the hypothesis suggested by McLaren (1960) that phocids were derived from a lutrine ancestry. The species evidently should be ranked as a very late development in sea otter evolution and one which shows very close affinity to the living species.

The multicusped, left, deciduous P_4 from the Timm's Point Silt (Early Pleistocene), which Mitchell (1966, p. 1909, figs. 4a–c) referred to *Enhydra* cf. *E. lutris*, allows little basis for direct comparison with the permanent dentition of *E. macrodonta*. Mitchell referred the Timm's Point fossil to the living species on the basis of obvious resemblance, but recognized that it differed from the compared specimens of *E. lutris* in being generally larger and in various details of occlusal morphology. The Timm's Point tooth was found to be slightly larger than two lower deciduous fourth premolars of *E. lutris* which were available in the present study (Table 1) and two others examined at the U. S. Geological Survey (Repenning, pers. comm. 1972). The fact that the deciduous tooth from Timm's Point Silt and the permanent premolars and M_1 of *E. macrodonta* are larger than their counterparts in *E. lutris* may be significant and open up the possibility that the Timm's Point fossil may be more closely related to *E. macrodonta* than to *E. lutris*. In addition, if the Late Pleistocene post-cranial elements described by Mitchell are indeed those of *E. lutris*, then it would appear probable that *E. macrodonta* and *E. lutris* coexisted in the northeastern Pacific during some part of the Pleistocene, perhaps as geographically separated populations.

The right M_1 of *E. macrodonta* shows a crude resemblance to the right M_1 of *Lutra reevei* Newton from the Norwich Crag (England) of Middle Pleistocene age, in having the same number and gross arrangement of cusps and ridges. It differs principally in having: 1) about twice the occlusal area; 2) a much squarer occlusal outline with a blunter anterior margin; 3) a paraconid that is proportionately smaller and lies more directly anterior to the protoconid; and 4) the protoconid

and metaconid positioned in a relatively more anterior position. These differences, taken in combination, would seem to indicate that *E. macrodonta* and *Lutra reevei* are not particularly closely related and that the M_1 of *L. reevei* was not a suitable morphologic structure for the derivation of M_1 in *E. macrodonta* in the interval from Middle to Late Pleistocene. Thus the author is in accord with Mitchell (1966) and Repenning (1967) that *L. reevei* is not ancestral to *Enhydra*. *Lutra reevei*, on the contrary, seems more closely allied to the Recent *Aonyx capensis* Schinz and the Pliocene *Enhydriodon africanus* Stormer, both from South Africa.

Adaptations: In comparison with *E. lutris* specimens of the same growth stage, the coronoid process in *E. macrodonta* is consistently shorter with respect to jaw length. This relationship suggests that the skull was not higher than *E. lutris* and may have been slightly lower.

Preserved insertional structures on the mandible of *E. macrodonta*, including those for the masseter, internal pterygoid, and temporal muscles, appear on the whole to be much less strongly formed than their counterparts in *E. lutris*. This circumstance suggests that the jaw musculature of *E. macrodonta* was generally less developed than that of the living species. If this line of reasoning is correct then it remains to be explained why *E. macrodonta* was endowed with substantially larger and heavier posterior teeth than is *E. lutris*. In theory this condition would seem to require that the jaw muscles of *E. macrodonta* would have to be more powerful than those for *E. lutris*, not less, as a comparison of the muscle insertion parts seem to suggest. No satisfactory explanation has been found for this apparent paradox.

It is possible that the musculature of *E. macrodonta* was, indeed, proportionately stronger than that of *E. lutris* but that: 1) the insertional structures do not reflect this condition, or 2) the insertional structures were not yet fully developed in the young adult of *E. macrodonta* and would be larger and more strongly formed in the fully adult state.

Environment of deposition: Enhydra macrodonta was recovered from a gray, clayey, finegrained sand containing the following molluscan species: *Yoldia* sp.; *Mytilus californianus*; *Clinocardium* sp.; *Macoma nasuta*; *Solen sicarius*; *Cryptomya californica*; *Teredo* (?) sp.; *Epitonium indianorum*; *Polinices lewisii*; *Thais lamellosa*; *Thais lima*; *Nassarius fossatus*; *Nassarius rhinetes*; and *Olivella biplicata*. The configuration of topographically higher exposures of Franciscan Forma-

tion rocks (Late Jurassic–Late Cretaceous), north and east of the Crannell Road deposit, indicate that the deposit probably accumulated in a semiprotected marine embayment along an open coast. The fossil assemblage and associated sediment indicate that the site of deposition was a muddy bottom which probably did not exceed five fathoms in depth. Some rocky outcroppings were located nearby.

Age: The recency of the otter-bearing deposit at Crannell Road is suggested by the following lines of evidence: 1) general lack of consolidation of the sediments and near horizontal attitude of bedding; 2) except for *Clinocardium* sp., which may be an extinct species, all the other mollusks in the otter-bearing deposit are presently living along the Humboldt County coast; and 3) fish otoliths found in the gray, pebbly sand, immediately below the otter-bearing unit (see description of the type locality above) are the same as those from the Palos Verdes Sand (Late Pleistocene) of San Pedro (Fitch, 1970).

Mammalian remains from the otter-bearing unit and from a marine deposit at Moonstone Beach, located 1½ miles north of Crannell Road, suggest somewhat greater precision in dating *Enhydra macrodonta*. From the pebbly, fossiliferous sand unit, which stratigraphically underlies the otterbearing unit, C. A. Repenning (pers. comm. to R. Kohl, 1972) has identified an upper premolar apparently inseparable from the sea lion, *Eumetopias jubata*. Repenning suggests that this tooth, based on limited material from other areas, is no older in age than Rancholabrean (Late Pleistocene). The Moonstone Beach deposit, which appears to contain a marine invertebrate fauna slightly older than that of the otter-bearing unit, has yielded the left scaphoid of a mammoth, *Mammuthus* sp. Repenning (pers. comm. 1972) considers this element to be no older in age than Irvingtonian (Middle Pleistocene), although it may be slightly younger.

Thus the available evidence points to a Rancholabrean or Late Pleistocene age for *Enhydra macrodonta*.

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